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RECIPROCAL TRANSLOCATIONS IN *DROSOPHILA* AND THEIR BEARING ON *OENOTHERA* CYTOLOGY AND GENETICS

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Belling¹ suggested that the chromosome rings found in *Oenothera* by Cleland² and others are to be explained as resulting from exchanges of ends between non-homologous chromosomes, so that one chromosome of a given complex is homologous at one end to one chromosome of a second complex, and at the other end to a different chromosome of the second complex. Håkansson³ and Darlington⁴ have elaborated this view. In a recent issue of this JOURNAL Cleland and Blakeslee⁵ have carried the analysis through in detail, showing that it gives self-consistent results. It enables one to predict the configurations of untried combinations, and is to a certain extent in agreement with the genetic data of Renner⁶ and Oehlkers.⁷

We have studied cases in *Drosophila* that conform to the scheme that is required to fit *Oenothera*. The details of these experiments are now ready for publication, and will appear elsewhere. We wish here to point out their bearing on *Oenothera* problems, since it has been possible to carry out a far more detailed and accurate genetic analysis than will be possible in *Oenothera* for many years.

We have studied four cases of translocations involving the two large V-shaped pairs of autosomes (II and III) of *Drosophila melanogaster*. One case (translocation *E*) apparently arose spontaneously. A section from the end of the left limb of chromosome II became detached, and re-attached near the middle of the left limb of chromosome III. This case, while of interest in other connections, does not furnish a good parallel to *Oenothera* and need not concern us further here. The other three cases (translocations *A*, *B* and *C*) all arose in x-ray experiments, and are all reciprocal translocations—i.e., they represent an exchange of parts

between chromosomes II and III. *A* and *C* are alike, *B* is of a somewhat different nature; they may be discussed separately.

In *A* and *C* both II and III broke at their mid-points (apices of the *V*'s, spindle-fibre attachment-points), and then the two left limbs became attached to each other, as did the two right limbs. If the normal chromosomes be designated II *L* II *R* (*L* = left limb, *R* = right limb) and III *L* III *R*, the new arrangement is II *L* III *L* and II *R* III *R*. Flies homozygous for the new arrangement do not survive—as is the case for the majority of the translocations found in *Drosophila*. Their death in the present instance, however, may be shown not to be due to the new arrangement of parts, since flies that receive translocation *A* from one parent and translocation *C* from the other are fully viable.

When flies heterozygous for translocations *A* or *C* and for the normal chromosome complement are mated to normal flies (with sufficient mutant characters present to mark all the chromosome segments concerned) only two types of offspring are produced—homozygous normal (from II *L* II *R*, III *L* III *R* gametes), and flies heterozygous for the translocation (from II *L* III *L*, II *R* III *R* gametes). Matings of translocation heterozygotes together show that four other types of gametes are formed and are functional—II *L* II *R*, II *L* III *L*, III *L* III *R*, II *R* III *R*, II *L* II *R* II *R* III *R*, and III *L* III *R* II *L* III *L*. These (which give inviable zygotes unless each meets its complementary class at fertilization) are produced in smaller numbers than are the first-named two types. The data indicate that about 60 per cent of all the gametes belong to the II *L* II *R* III *L* III *R* and II *L* III *L* II *R* III *R* classes—a result which checks exactly with the independent observation that, from normal female crossed to heterozygous translocation male, about 60 per cent of the eggs give viable offspring, and about 40 per cent die in early stages. Crossing-over occurs in all regions in females heterozygous for these translocations, but is appreciably less than in normal flies.

The cytological picture shows four *V*-shaped chromosomes, as in normal *melanogaster*; but the somatic pairing, characteristic of the *Diptera*, is upset. In no case have we seen two pairs each with both members parallel—as is the commonest arrangement in normal flies. In two figures there was a cross-shaped arrangement, each arm of each chromosome paired with another arm, but these two other arms belonging to different chromosomes. The other figures seen approximated more or less closely to this arrangement, which is the one the genetic results led us to expect. The maturation divisions have not been studied; we do not know whether or not rings of the *Oenothera* type are present, but they may be expected.

In translocation *B*, chromosome III broke at its mid-point, chromosome II somewhat to the left of its middle, and again the two left portions united as did the two right ones. Here the cytological results show one unusually

long chromosome and one short one, with a disturbance of the somatic pairing. The most important difference in the genetic results is that *B* gives more irregular gametes than do *A* and *C*. The gametes formed are II *L* II *R* III *L* II *L* and III *R* II *R* III *L* III *R*, not the other two types (III *R* II *R* II *L* II *R* and III *L* II *L* III *L* III *R*), since the composite including more than a half of II always passes to the opposite pole from the normal II. In agreement with this result is the fact that only 47 per cent of the eggs from normal females fertilized by males heterozygous for translocation *B* were viable, as opposed to the 60 per cent from *A* and *C*.

In general, translocations *A* and *C* furnish clear models for the Belling scheme, while *B* and *E* do not give results that so closely parallel the behavior of *Oenothera*. One may infer that the *Oenothera* translocations represent exchanges of equal portions—very probably halves—of chromosomes. This is in agreement with the observation that there are no appreciable size differences among the chromosomes of *Oenothera*.

That crossing-over occurs in flies heterozygous for the translocations is consistent, for it is difficult to avoid the conclusion that such *Oenothera* types as the sulfur-flowered forms of *biennis* and *suaveolens* arise through crossing-over within chromosome rings. There are also indications that crossing-over is more frequent in the paired chromosomes of *Oenothera* than in the rings—just as it is more frequent in normal *Drosophila* than in heterozygous translocation flies.

That translocations in *Drosophila* are frequently lethal in homozygous form when they first arise is suggestive in view of the well-known fact that the majority of the *Oenothera* complexes carry zygote lethals. One may surmise that the lethals and the rearrangements of parts of chromosomes arose simultaneously.

One difference between the cases here described and those in *Oenothera* is that the irregular types of gametes are functional in *Drosophila*, whereas in *Oenothera* they evidently are represented by the empty pollen-grains and ovules. The difference is, obviously, to be referred to the relatively more complex development of the haploid stage in plants than in animals.

Translocations *A* and *C* furnish all the necessary requirements for the Belling interpretation, and it has been possible to analyze them in great detail. We feel confident that the Belling interpretation is essentially correct for *Oenothera*, both because of this definitely established parallel case and because of the power of prediction that arises from it.

¹ Belling, J., 1927. "The Attachment of Chromosomes at the Reduction Division in Flowering Plants." *J. Genet.*, 18, 177–205.

² Cleland, R. E., 1923. "Chromosome Arrangements during Meiosis in Certain *Oenothera*." *Am. Nat.*, 57, 562–566.

³ Håkansson, A., 1928. "Die Reduktionsteilung in der Samenanlage einiger *Oenotheren*." *Hereditas*, 11, 129–181.

⁴ Darlington, C. D., 1929. "Ring-Formation in *Oenothera* and Other Genera." *J. Genet.*, **20**, 345-363.

⁵ Cleland, R. E., and A. F. Blakeslee, 1930. "Interaction between Complexes as Evidence for Segmental Interchange in *Oenothera*." *Proc. Nat. Acad. Sci.*, **16**, 183-189.

⁶ Renner, O., 1925. "Untersuchungen über die faktorielle Konstitution einiger komplexheterozygotischen *Oenotheren*." *Bibliotheca Genetica*, **9**, 1-168.

⁷ Oehlkers, F., 1926. "Erblichkeit und Zytologie einiger Kreuzungen mit *Oenothera strigosa*. (Vererbungsversuche an *Oenotheren* 4)." *Jahrb. wissenschaft. Botanik*, **65**, 401-446.

NOTES ON THE PLASTID AND OTHER CYTOPLASMIC BODIES
DURING SPOROGENESIS AND SPERMATOGENESIS IN
POLYTRICHUM COMMUNE

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The question of the nature, the value and the function of cytoplasmic bodies cannot be settled unless we possess an exact account of the behavior of such bodies throughout the complete life history of a plant form. Because such an account is lacking the author has undertaken to study the stages of development from spore to spore in the mosses *Polytrichum commune* and *Catharinea undulata*. On account of possible alterations due to fixation, careful comparisons are being made between the effects of killing solutions such as Bouin and Flemming, and the more specialized techniques, Regaud, Benda, Kolatchev, and Da Fano. The studies on fixed cells are being controlled as far as possible by studies on living material.

Some points have already been well established by others but many questions remain unsettled. That the chloroplast persists during sporogenesis was demonstrated by the work of Sapěhin. However, little is definitely known of the origin of the archesporial plastid, of its division in the archesporial line; and of its behavior during meiosis and in the development of the spore. The relation of the mitochondria and the plastid during sporogenesis is a second question, which has been rather obscured by the recent work of Senjaninova.¹ No botanist has as yet concerned himself with the development of the plastid or of other cytoplasmic bodies in the archeogonium. Allen's² account of spermatogenesis undoubtedly gives as much detail as it was possible to obtain with fixing solutions containing acetic acid. But, in view of the recent work on animal spermatogenesis, there is much in the account of sperm development